

Mortality and Recruitment of Pacific Sardine, *Sardinops sagax caerulea*, Larvae in the California Current

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Butler, J. L. 1991. Mortality and recruitment of Pacific sardine, *Sardinops sagax caerulea*, larvae in the California Current. *Can. J. Fish. Aquat. Sci.* 48: 1713–1723.

The mortality rates of Pacific sardine, *Sardinops sagax caerulea*, larvae (<20 d) increased during 1951–67, and this increase was positively correlated with the increase in biomass of northern anchovy, *Engraulis mordax*. Other potential correlates with larval sardine mortality rates were examined using multiple correlation. These included temperature and zooplankton volumes at stations positive for sardine larvae, water column stability, upwelling, transport, salinity anomalies, and Pacific mackerel, *Scomber japonicus*, abundance. None contributed significantly to the multiple regression with anchovy abundance. Thus, no evidence existed for either Lasker's stable ocean hypothesis of larval mortality or Hjort's larval transport hypothesis. The logarithm of the ratio of sardine recruits at age 2 to the spawning biomass was used as an index of recruitment success. Sardine recruitment success at age 2 was not correlated with larval mortality rates. Sardine recruitment, however, was negatively correlated with both northern anchovy biomass and the combined biomass of Pacific sardine, Pacific mackerel, and northern anchovy. A plausible explanation for this result is that predation by pelagic fishes results in greater mortality rates of sardine larvae and juveniles which in turn decrease sardine recruitment.

De 1951 à 1967, les taux de mortalité de larves (< 20d) de sardine du Pacifique (*Sardinops sagax caerulea*) ont montré une augmentation en corrélation positive avec l'augmentation de la biomasse d'anchois du Pacifique (*Engraulis mordax*). L'auteur a utilisé une corrélation multiple pour étudier d'autres facteurs potentiels en corrélation avec les taux de mortalité des larves de sardine, en particulier la température et les volumes de zooplancton présents aux stations fréquentées par des larves de sardine, la stabilité de la colonne d'eau, les remontées d'eau profonde, le transport, les anomalies de la salinité et l'abondance du maquereau (*Scomber japonicus*). Aucun de ces facteurs n'a contribué de façon significative à la régression multiple en fonction de l'abondance de l'anchois. L'hypothèse de l'océan stable de Lasker concernant la mortalité des larves et l'hypothèse du transport des larves de Hjort ne sont donc pas étayées. L'auteur utilise le logarithme du rapport entre le nombre de recrues de sardine de 2 ans et la biomasse de reproducteurs comme indice du succès du recrutement. Le succès du recrutement de sardines de 2 ans n'est pas en corrélation avec les taux de mortalité des larves. Par contre, le recrutement des sardines est en corrélation négative avec la biomasse d'anchois du Pacifique et la biomasse combinée de la sardine, du maquereau et de l'anchois. Une explication plausible de ce résultat serait que la prédation exercée par les poissons pélagiques est la cause de taux de mortalité plus élevés des larves et des juvéniles de sardine, qui ont pour résultat une baisse de son taux de recrutement.

Received May 16, 1988
Accepted March 13, 1991
(J9734)

Reçu le 16 mai 1988
Accepté le 13 mars 1991

The causes of larval fish mortality have been the subject of considerable speculation for several decades. Most speculation is on the relative importance of starvation or predation in determining the mortality rate of larvae.

The starvation hypothesis is based in part on the observation that larval fish reared in the laboratory require greater food densities than are generally found in the ocean. Field and laboratory experiments (Hjort 1913, 1926; Lasker 1975) have supported the idea that the availability of food affects the survival of first-feeding larvae. The incidence of starving larvae of northern anchovy, *Engraulis mordax*, and jack mackerel, *Trachurus symmetricus*, in plankton net collections suggests that starvation mortality is restricted to the first 1–2 wk after yolk sac absorption (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986).

The basis of the predation hypothesis is that larval fish are minor constituents of the zooplankton community and that a great many zooplankton and planktivorous fishes eat larval fish. Moreover, eggs and yolk-sac larvae that have internal food sup-

plies and do not die from starvation sustain mortality rates which are greater than first-feeding larvae, and this mortality can be due only to predation (Hunter 1984). Egg and larval predators have been identified in the field, and losses due to predation by copepods (Lillelund and Lasker 1971; Brewer et al. 1984), euphausiids (Theilacker and Lasker 1974; Brewer et al. 1984), amphipods (Brewer et al. 1984); jellyfish (Möller 1984; Van der Veer 1985; Purcell et al. 1987), cnidarians and ctenophores (Purcell 1985), and fish (Frank and Leggett 1984; Alheit 1987) have been assessed. Planktivorous fish have been considered to be the cause of as much as 50% of the observed mortality of eggs of the Peruvian anchoveta, *Engraulis ringens* (Alheit 1987).

The objectives of this study were to (1) examine larval mortality rates of the Pacific sardine, *Sardinops sagax caerulea*, population, (2) compare these rates with the mortality rates of northern anchovy during the same period, and (3) investigate interannual variation of larval sardine mortality rates. Three possible hypotheses to explain annual variation in larval sardine

mortality rates were investigated. These were the stable ocean hypothesis (Lasker 1978, 1981) which proposes that periods of calm weather are necessary to allow first-feeding larvae to find aggregated food patches, the transport hypothesis (Hjort 1913) which proposes that currents may sweep larvae out of suitable feeding areas, and the predation hypothesis (Hunter 1984) which proposes that the abundance of predators on eggs and larvae will affect mortality rates.

These hypotheses were further tested to determine whether any factor can be used to predict recruitment. The potential predators of eggs and larvae that I considered were adult northern anchovy, Pacific sardine, and Pacific mackerel, *Scomber japonicus*. Jack mackerel were excluded as a potential predator because of their offshore distribution.

Methods

Larval Mortality

I estimated sardine larval mortality rates from the decrease in numbers of larvae in successive size intervals found in 1-m, 500- μ m-mesh oblique ring net tows collected by the California Cooperative Oceanic Fisheries Investigation (CalCOFI). Size-frequency distributions of larvae from 3.9 to 16.2 mm were converted to age-frequency distributions using growth rates determined in the laboratory for yolk-sac larvae and in the field for feeding larvae.

Oblique net tows were taken during a series of monthly cruises beginning in 1951 and ending in 1966. Quarterly CalCOFI cruises were initiated in 1961. After 1967 the numbers of sardine larvae collected were insufficient for estimating mortality rates.

Abundance in each length class was estimated using a weighted negative binomial model (Bissell 1972; Zweifel and Smith 1981; Lo 1985). I adjusted the numbers of larvae in ichthyoplankton net collections for the following possible biases: extrusion through the mesh (Lenarz 1972, 1973; Lo 1983), day-night difference in avoidance (Lo 1985), and volume of water filtered at each depth (Kramer et al. 1972).

Duration of yolk-sac stage was determined from temperature-dependent growth rates calculated using the model of Zeifel and Lasker (1976). Sardine larvae hatch 2.24 d after fertilization at 17°C and reach the first-feeding stage in 5 d at a larval length of 6.2 mm (Zweifel and Lasker 1976). As we know from daily increments in their otoliths, sardine larvae reach a length of 15 mm (live standard length) in about 23 d after hatching (Butler and de Mendiola 1985; Castillo et al. 1986; Butler 1987).

Because estimates of the ages of fish larvae stored in formalin for more than 20 yr are unattainable from otoliths, I estimated ages by the duration of each length interval from growth rates back-calculated from increment widths in the otoliths of juveniles hatched in each month of the year (Butler 1987). The daily formation of these increments was demonstrated by Butler and de Mendiola (1985) and Butler (1987). I used a Laird-Gompertz curve to describe the growth rates of larval sardine:

$$(1) L_t = L_\infty [L_{ff}/L_\infty] e^{-a_m(t-ff)}$$

where L_t is the live length at age t days from first feeding, L_∞ is the asymptotic length at metamorphosis = 35 mm, L_{ff} is the length at first feeding and first increment formation = 6.2 mm, a_m is the seasonally dependent growth coefficient, and t is the time from first feeding in days or the number of daily increments.

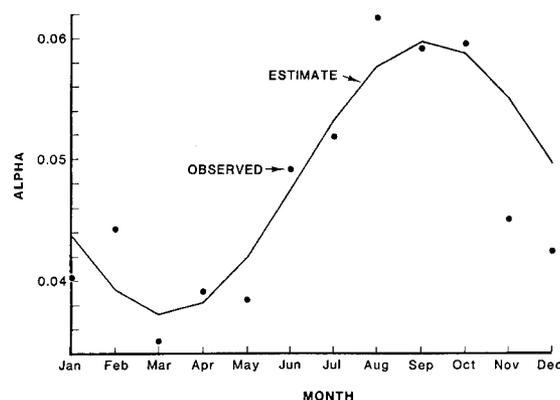


FIG. 1. Seasonal variation in larval growth parameter of the Pacific sardine. Smooth curve is sine function fitted to the data. See text for equation.

I used a sine curve to describe the seasonal growth coefficient (L_m) of the Gompertz curve (Laird 1967):

$$(2) a_m = 0.0485 + 0.00113 \cdot \sin(\text{month} - 6.182) \cdot 0.5234.$$

I fitted equation (2) nonlinear regression, weighting the value of alpha of each month by the number of observations for that month (Fig. 1).

Survivorship of sardine larvae increases with age. Survivorship (S) at a given time (t) can be modeled using a Pareto hazard function:

$$(3) S(t) = (t/u)^{-\beta}$$

where u is the time of hatching (Lo 1985). The observed mean daily production of larvae y_i is related to survivorship by

$$(4) y_i = y_u(t/u)^{-\beta}.$$

β was estimated by taking the logarithm of both sides of the equation:

$$(5) \ln(y_i) = B - \beta \ln(t/u).$$

Unlike that for anchovy, sardine mortality begins to decline at hatching. I used eight size intervals from hatching to a live size of about 15 mm to estimate β . I compared annual estimates of β for sardine larvae with the annual β for anchovy larvae estimated by Lo (1985) for the same geographic area.

Stable Ocean Hypothesis

To test the stable ocean hypothesis (Lasker 1975, 1981) that larval mortality rates are influenced by stability of the water column, I followed the procedure of Peterman and Bradford (1987), which is to correlate mortality rates with an index of water column stability.

To choose an appropriate stability index, I estimated a geographic center of sardine spawning from the position of positive plankton tows weighted by the number of sardine larvae in each tow. From 1951 to 1967 the latitude of the center of spawning varied from 25°56.4'N in 1965 to 32°11.4'N in 1959, with the overall mean at 28°24.5'N off northern Baja California (Table 1). Since wind data were not available for 29°N, stability indices were calculated from daily average wind speed at

TABLE 1. Geographic distribution of Pacific sardine larvae during 1951–67. Center of distribution is mean position of positive tows weighted by the number of larvae. Southern and northern positions are latitudinal limits of distribution.

Year	Center		Southern		Northern	
	Latitude North	Longitude West	Latitude North	Longitude West	Latitude North	Longitude West
1951	27°52.0'	115°24.7'	22°47.5'	110°22.0'	36°39.0'	122°26.0'
1952	27°59.6'	115°11.1'	24°19.0'	111°48.0'	35°57.0'	119°11.0'
1953	28° 4.3'	115°12.5'	25°33.3'	112°15.5'	34° 9.5'	119°31.8'
1954	29° 8.6'	116° 0.4'	24°21.3'	111°49.0'	35°54.3'	122°22.7'
1955	29°35.6'	116°40.3'	22°35.0'	110°15.1'	34° 8.5'	121° 9.0'
1956	29°10.1'	116° 1.9'	23°55.5'	111° 5.0'	33°47.7'	118°41.0'
1957	29°47.1'	115°55.0'	25°33.5'	112°18.0'	36°39.0'	122°26.0'
1958	31°24.8'	117° 2.4'	24°11.0'	112° 3.0'	36° 9.0'	121°50.0'
1959	32°11.4'	117°50.7'	23°56.0'	111° 4.2'	37°21.0'	124°22.0'
1960	31°10.4'	117°32.4'	24°19.0'	111°48.0'	34°15.2'	119°58.3'
1961	29°31.8'	115°40.6'	25°33.4'	112°18.5'	35°31.7'	121°25.2'
1962	28°27.8'	115°10.9'	26° 4.5'	112°48.0'	36°16.0'	121°40.0'
1963	29°26.1'	115°19.6'	25°38.0'	112°11.2'	36°10.7'	121°45.6'
1964	27°27.9'	113°36.2'	24° 2.0'	113°41.5'	35°38.2'	121°14.2'
1965	25°56.4'	112°27.2'	24°47.4'	112°20.3'	36°54.4'	121°52.9'
1966	27°33.6'	113°31.1'	25°33.6'	112°18.7'	36°10.4'	121°45.9'
1967	29° 0.1'	114°54.0'	25°34.0'	112°19.0'	31°42.1'	116°43.4'

30°N and 116°W. This wind speed index was determined from the number of consecutive 4-d periods of calm weather per month, derived from marine observations from 1953 to 1967.

Based on the analysis of Simpson and Dickey (1981), I used a wind speed of 10 m/s as a cutoff between calm weather and turbulent mixing. Wind speeds greater than 10 m/s produce turbulent mixing in the upper mixed layer which, according to Lasker (1975), should disrupt patches of microzooplankton necessary for successful first feeding of anchovy larvae. The stability index for each month was weighted by the monthly proportion of the annual production of sardine larvae. Missing values of larval production (35 of 204 months) were estimated from adjacent values.

Transport Hypothesis

In the California Current, transport has two components: a southerly component and a seasonal offshore component. To investigate Hjort's hypothesis that transport away from nursery grounds during the larval phase contributes to mortality of larvae, I calculated two indices of transport. Sea level has been shown to be an index of changes in the southerly transport of the California Current (Chelton 1980; Chelton et al. 1982), and offshore Ekman transport is an index of offshore transport (Parrish et al. 1981; Bakun 1985). Each index for each month was weighted by the monthly proportion of the annual production of sardine larvae.

Although no sea level index is available for the center of sardine spawning, the anomalies at one locality are strongly correlated with anomalies at other localities along the coast (Chelton 1980). Thus, the index calculated for San Diego may be considered representative of northern Baja California.

To investigate whether interannual variability in offshore transport influenced the observed increase in larval sardine mortality rates, I calculated an annual index of upwelling at 31°N, 119°W from monthly upwelling indices (Bakun 1973), weighted by the monthly proportion of the annual production of larvae.

Predation Hypothesis

To investigate the hypothesis that the total abundance of coastal pelagic planktivorous fishes affects larval sardine mortality rates, I regressed β on estimates of the total biomass of Pacific sardine by MacCall (1979), Pacific mackerel by Parrish and MacCall (1978), and northern anchovy by Methot (1986). I also regressed β on the biomass estimates of each species. Estimates of total sardine biomass (Table 2) and biomass of recruits at age 2 are from virtual population analysis estimates derived from landings and are independent of the number of sardine eggs and larvae in plankton samples.

The abundance of alternative prey has been proposed to affect the strength of predation by pelagic fish on larval fish (Pepin 1987). To test this hypothesis, I calculated a predator to prey ratio from the total biomass of pelagic fish and zooplankton volumes (Table 3).

To investigate the hypothesis that the abundance of predators affects recruitment through predation on young-of-the-year sardines, I regressed an index of recruitment against the total biomass of coastal pelagic fishes (as defined above) with a 2-yr time lag. The index that I used was the logarithm of the ratio of sardine recruits at age 2 to spawning biomass. Thus, the abundance of predators during the year of spawning was compared with the strength of recruitment 2 yr later. This index was also compared with the biomass of each species to detect any interspecific effects.

Correlation Analyses

Since correlation analysis cannot reveal cause and effect, any correlation may be a result of a correlation with another variable. To test for alternative hypotheses, I performed a stepwise multiple correlation of β and recruitment success on several factors. These factors included temperatures at 10 m (Table 4), zooplankton volumes, latitude of center of spawning, Scripps Pier salinities, sea level anomalies, wind speed indices, upwelling indices, anchovy biomass, Pacific sardine biomass, and Pacific mackerel biomass. Small zooplankton volumes, rou-

TABLE 2. Time series of estimated larval mortality coefficients and total biomass estimates (metric tons, t) of Pacific sardine and northern anchovy during 1951–67.

Year	Pacific Sardine			Northern anchovy			Total biomass (10 ³ t) ^c
	Biomass (10 ³ t) ^a	Larval β	SE	Biomass (10 ³ t) ^b	Larval β	SE	
1951	277	1.74	0.18		0.85	0.15	277
1952	136	2.02	0.25		0.88	0.20	136
1953	202	1.54	0.34		0.95	0.10	202
1954	239	1.77	0.30	45	1.16	0.24	284
1955	170	2.66	0.18	32	1.01	0.17	202
1956	108	2.23	0.33	24	0.88	0.20	131
1957	90	1.65	0.40	88	0.94	0.10	178
1958	177	2.53	0.18	146	0.88	0.08	323
1959	122	2.69	0.18	111	1.18	0.06	233
1960	88	2.35	0.21	66	1.80	0.23	154
1961	54	2.71	0.42	130	1.55	0.16	184
1962	27	2.77	0.36	194	1.08	0.23	221
1963	21	3.79	0.23	204	0.81	0.04	225
1964	11	3.07	0.21	235	1.44	0.21	246
1965	3	3.54	0.28	257	2.42	0.12	260
1966		3.63	0.15	226	1.84	0.04	226
1967		3.77	0.23	195	2.15	0.08	195

^aFrom MacCall (1979).

^bFrom Methot (1986).

^cFrom Lo (1985).

TABLE 3. Annual weighted mean volume of small zooplankton (cm³/1000 m³) in 1-m net tows positive for sardine larvae. Mean value weighted by number of sardine larvae collected in tow.

Year	Mean	SD	Low	High
1951	113	63	13	609
1952	154	125	17	1144
1953	168	112	15	1058
1954	145	122	16	1660
1955	209	354	17	6509
1956	289	240	17	1875
1957	165	110	13	2298
1958	110	71	9	532
1959	100	103	7	646
1960	227	164	10	1814
1961	157	93	6	652
1962	164	174	17	1071
1963	382	270	17	1231
1964	225	289	17	1547
1965	372	132	14	977
1966	211	73	17	926
1967	367	272	5	2215

tinely measured in the CalCOFI program, are the displacement volumes of the zooplankton taken in ichthyoplankton tows after large gelatinous organisms, such as medusa and salps with individual volumes exceeding 5 mL, are removed (Kramer et al. 1972). These volumes are assumed to be a measure of potential predators rather than larval food which must be collected with 75- μ m-mesh nets (Owen et al. 1990).

Temperature, zooplankton volumes, and the geographic positions were weighted by the number of sardine larvae at each station. Weighting produces values representative of the environment experienced by most sardine larvae, but it is not confounded with mortality, which is calculated from abundance of larvae in length classes without regard to their geographic position.

TABLE 4. Annual weighted mean temperature of stations positive for Pacific sardine larvae during 1951–67. Temperature at each station weighted by the number of larvae collected at that station.

Year	Temperature (°C)				Stations	Larvae
	Mean	Low	High	SD		
1951	16.8	11.3	26.4	2.5	162	6059
1952	17.1	11.2	24.4	1.9	203	5512
1953	16.7	12.1	25.2	2.1	175	3414
1954	16.4	12.9	23.7	2.0	355	7108
1955	15.6	12.8	20.2	1.2	255	4358
1956	17.5	11.9	27.4	3.5	169	2692
1957	19.1	13.0	24.8	2.8	173	2712
1958	19.0	11.9	27.3	2.5	193	3824
1959	18.7	12.7	25.0	3.2	170	2079
1960	19.4	10.7	25.0	2.4	138	3723
1961	17.3	12.6	22.0	1.7	53	761
1962	17.7	12.8	23.0	2.2	57	1006
1963	19.7	10.9	24.6	3.2	99	2141
1964	19.6	12.2	25.2	2.9	86	4892
1965	23.2	11.3	26.5	2.0	105	12272
1966	22.4	11.8	24.7	3.2	139	4900
1967	15.7	13.0	20.7	1.8	24	684

The testing of the significance of correlation coefficients assumes that each observation in the data set is independent. For time series, this requires that the autocorrelation coefficients be small for lag periods greater than zero. This is not the case for time series of populations with generation times greater than the periodicity of sampling. Thus, the time series of anchovy biomass and β are both autocorrelated at a time lag of 1 yr ($R = 0.793$ for anchovy and $R = 0.631$ for β). For autocorrelated time series, Bayley and Hammersley (1946) have proposed a corrected number of independent observations, N^* :

$$(6) \quad 1/N^* = 1/N + 1/N^2 \sum_{j=1}^{N-1} (N-j) [P_j \tau_j]^2$$

where N is the total number of observations and (P, τ) is the autocorrelation coefficient of the j^{th} lag of period. Blackman and Tukey (1958) suggested that j not exceed $1/10 N$ because of the small number of observations included in the autocorrelations as j approaches $(N - 1)$. The significance levels that I use are based on Bayley and Hammersley's (1946) procedure as modified by Blackman and Tukey (1958) (see also Sutcliffe et al. 1976).

Results

Larval Mortality

The log transform for abundance as a function of age is best fit with a straight line (Fig. 2). Thus, the probability of survival of sardine larvae increases with age. The age-specific mortality coefficient, β , varied during 1951–67 (Table 2). The mean value for the 17-yr time series was 2.61 and the variance was 0.562.

Mortality rates of sardine larvae were significantly greater than those of anchovy larvae in the same area in 14 of 17 yr during 1951–67 (Fig. 3). Survival from yolk-sac larvae to 20-mm larvae ranged from 0.05 to 3.1% during 1951–67. During the same period, survival of anchovy larvae from first feeding to 19 mm length ranged from 0.2 to 10.6% (Lo 1985).

Stable Ocean Hypothesis

The estimated mortality rates of sardine larvae showed no relationship to the stability of the water column during 1951–66. There was no significant correlation ($R^2 < 0.03$, $N^* = 14$, $P > 0.37$) with the weighted index of calm weather and the larval sardine mortality coefficient, β .

Salinities of seawater have been correlated with the catch of 3-yr-old Pacific sardine (Walford 1946). This correlation was over a limited time series and attempted to relate the apparent year-class size of Pacific sardine to salinity as an index of upwelling, and hence food availability. Neither larval sardine mortality coefficient, β , calculated here, nor sardine recruitment was correlated with either annual mean Scripps Pier salinities or the annual anomaly from 1951 through 1967 ($R^2 = 0$, $N^* = 14$, $P > 0.10$). Thus, no support was found for the hypothesis that salinity as an index of upwelling affects larval mortality or predicts recruitment.

Transport Hypothesis

Advection of fish larvae away from coastal nursery areas may lead to higher mortality. However, neither the mortality rate of sardine larvae ($R^2 = 0.20$, $N^* = 15$, $P = 0.09$) nor the recruitment of 2-yr-olds ($R^2 = 0.08$, $N^* = 12$, $P = 0.37$) was correlated with the upwelling index at 31°N. Thus, this time series does not support the hypothesis that offshore transport is a determining factor of mortality rates in Pacific sardine larvae.

The mortality rate of sardine larvae showed no correlation ($R^2 = 0.03$, $N^* = 14$, $P > 0.10$) with the sea level anomaly as an index of transport. However, the recruitment of 2-yr-olds showed a positive correlation ($R^2 = 34.3$, $N^* = 13$, $P < 0.05$) with the average sea level anomaly during 1951–67. If the average sea level anomaly is compared with recruitment using a 2-yr time lag, to test the effect of southerly transport during the year that the eggs were spawned, then the correlation is negative, but not significant ($R^2 = 0.074$, $N^* =$

13, $P > 0.10$). Evidence for the hypothesis that southerly transport determines sardine recruitment will be discussed below.

Predation Hypothesis

A corollary of the predation hypothesis is that mortality rates of fish larvae should increase when predator abundance increases. Important predators of planktonic larvae are other zooplankton and planktivorous fish. The mortality of sardine larvae increased in years of high zooplankton volumes (Table 3). Small zooplankton biomass was associated with 36% of the interannual variability of sardine larval β ($N^* = 12$, $P < 0.05$). This indicates a positive relationship between mortality rates and the abundance of zooplankton predators.

Mortality rates of sardine larvae increased over the period 1951–67 (Fig. 3). The biomass of northern anchovy also increased during this period (Table 2). Mortality rates of sardine larvae were positively correlated with anchovy abundance (Fig. 4). The increase in biomass of northern anchovy accounted for 58% of the interannual variability of larval sardine mortality rates ($N^* = 6$, $P < 0.01$).

The abundance of alternative prey affects the strength of fish predation on larval fish. The mortality rate of sardine larvae was positively correlated with the predator prey ratio (pelagic fish biomass/zooplankton volumes) ($R^2 = 0.47$, $N^* = 12$, $P < 0.01$).

Total pelagic fish biomass was significantly negatively correlated with the index of sardine recruit-per-spawn lagged by 2 yr ($R^2 = 0.39$, $N^* = 12$, $P = 0.03$). This correlation is not simply due to a similar time trend in both variables. Pelagic fish biomass varied with a cyclic pattern from 1951 to 1962 (Fig. 5). This time series was significantly negatively autocorrelated at a time lag of 2 yr. The recruitment index of Pacific sardine varied in a similar, but opposite, cycle from 1951 to about 1958. Afterwards, recruitment remained low through 1962.

Biotic factors, rather than abiotic factors, appear to affect larval sardine mortality. The relationship between anchovy biomass and zooplankton biomass seems to explain the observed interannual variability in sardine mortality rates. Larval sardine mortality rates were significantly negatively correlated with both anchovy biomass ($R^2 = 0.63$, $N^* = 8$, $P = 0.001$) and zooplankton biomass ($R^2 = 0.40$, $N^* = 14$, $P = 0.01$). However, larval sardine mortality rates were not correlated with either the total Pacific mackerel biomass ($R^2 = 0.01$, $N^* = 13$, $P > 0.10$) or with the biomass of Pacific mackerel recruits (data from Parrish and MacCall 1978).

The dominant period of the oscillations in pelagic fish biomass (Fig. 5) is 2 yr. This is about the life span of the northern anchovy. To investigate whether northern anchovy affects sardine recruitment, I performed a stepwise multiple correlation analysis on total pelagic fish and anchovy biomass. In this analysis, anchovy biomass was more strongly correlated with sardine recruitment than total pelagic fish biomass ($R^2 = 0.37$, $N^* = 6$, $P = 0.08$). Because of the significant correlation between total pelagic fish biomass and anchovy biomass, it is difficult to separate the two hypotheses that predation by northern anchovy or predation by all pelagic fish on late larvae and juvenile sardines determines recruitment. However, the predation hypothesis is supported by this analysis.

Alternative Hypotheses

The correlations found in the preceding sections may not be due to cause and effect but rather to correlations with some

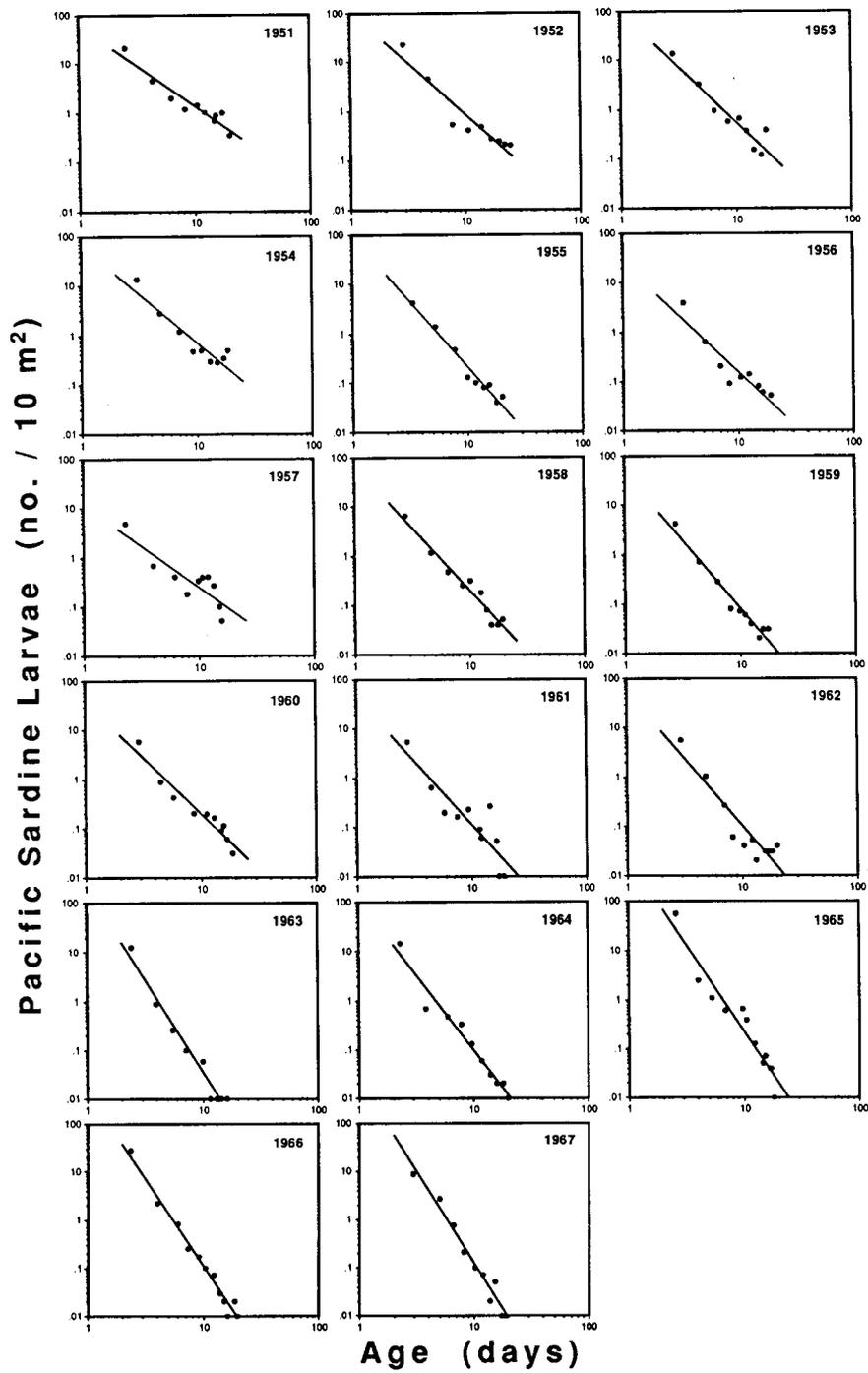


FIG. 2. Abundance of Pacific sardine larvae as a function of age for 1951-67.

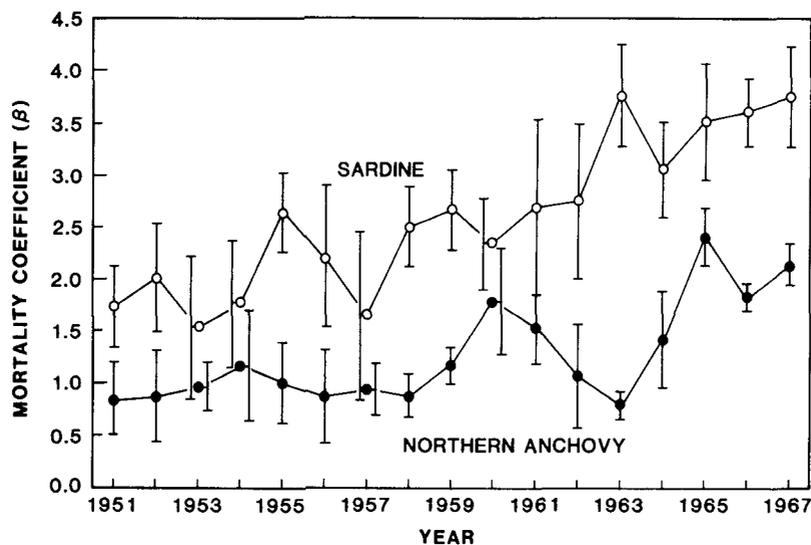


FIG. 3. Increase in the larval mortality coefficient, β , during 1951–67 for Pacific sardine and northern anchovy.

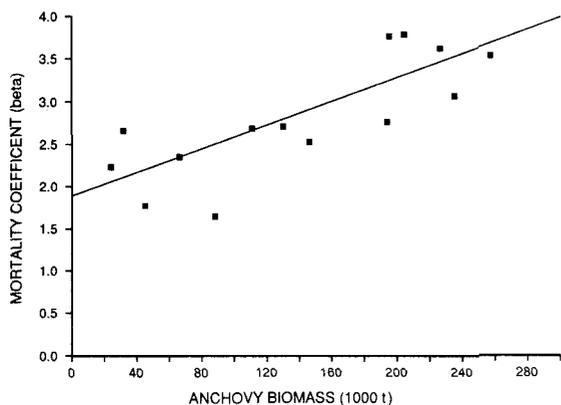


FIG. 4. Correlation of interannual variation of the larval mortality coefficient, β , of Pacific sardine and total biomass of northern anchovy.

other factor which affects mortality and recruitment. To test for an alternative explanation, I performed correlation analyses with some of the other factors which might be operating. These were temperature, geographic locality, small plankton abundance, salinity, turbulent mixing, and offshore transport.

Because larval sardine growth rates are correlated with temperature (Castillo et al. 1986) and growth rates determine the duration of larvae in each length class, temperature may affect mortality in an important way. Temperature is also used to calculate embryonic growth rates, which are then used to calculate mortality rates ($dN/dt = dN/dL \cdot dL/dt$ where dL is a length interval); a positive correlation with mortality rates is expected if temperature is confounded with mortality rates. However, lower temperature may slow the rate of development and extend

the time that larvae experience high mortality at small sizes. Thus, a negative relationship between mortality and temperature is also conceivable. At stations yielding sardine larvae, temperatures ranged from 10.7 to 27.4°C. The annual weighted means ranged only from 15.6 to 23.2°C (Table 4). These temperatures were not significantly correlated with larval sardine mortality rate ($R^2 = 0.172$, $N^* = 15$, $P > 0.10$). Thus, I reject temperature as an important factor contributing to larval mortality.

To investigate whether there were significant interactions between mortality rates and any other variable, I tested the relationship using stepwise multiple correlation with temperature, latitude, small plankton volume, and Scripps Pier salinity anomalies, an index of turbulent mixing derived from wind data, an index of offshore transport, and the biomass of sardine, the biomass of anchovy, and the biomass of Pacific mackerel. The only significant correlation detected was between larval sardine mortality rates and anchovy biomass, and this correlation was positive. The coefficient of determination of β and anchovy biomass was 0.63 ($N^* = 9$, $P = 0.001$). The multiple correlation of β and anchovy biomass and small zooplankton volumes as a second correlate was not significant ($R^2 = 0.74$, $N^* = 9$, $P = 0.07$). Thus, the abundance of anchovy is the most important variable tested that explains the interannual variability in larval sardine mortality rates.

Larval mortality rates are only one factor in the process of recruitment. Because sardines enter the fishery at age 2, considerable mortality must occur between the larval phase and recruitment. To test whether larval mortality rates are a predictive indicator of recruitment, I regressed them against biomass at age. The association was not significant, although the sign of the relationship was negative as expected.

To investigate whether recruitment declined due to density-dependent effects on larval mortality rates (β), I regressed the logarithm of ratio of recruits at age 2 and the spawning biomass lagged by 2 yr as an index of recruitment success on both sar-

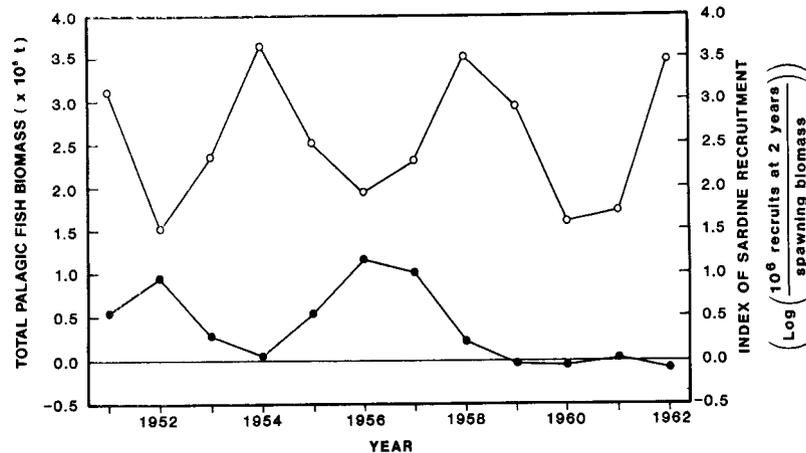


FIG. 5. Time series of total pelagic fish biomass (open circles) (Pacific sardine, northern anchovy, and Pacific mackerel) and recruitment index (solid circles) of Pacific sardine.

dine spawning biomass and β . Neither sardine biomass ($N^* = 11$, $P = 0.717$), nor β ($N^* = 10$, $P = 0.16$), nor the two variables in combination predicts recruitment success.

I also tested whether any other environmental factor was a reliable predictor of recruitment success: temperature, zooplankton volumes, latitude of center of spawning, sardine biomass, anchovy biomass, Pacific mackerel biomass, total pelagic fish biomass (anchovy, sardine, and Pacific mackerel), average sea level anomaly, and wind speed index. Again, total pelagic fish biomass ($N^* = 12$, $P = 0.03$) and anchovy biomass ($N^* = 9$, $P = 0.08$) were significantly negatively correlated with sardine recruitment success. Thus, no environmental factor, other than the abundance of predators, predicts sardine recruitment success.

Discussion

Larval Mortality

The mortality of Pacific sardine larvae was greater than that of northern anchovy larvae from 1951 to 1967 ($T = 9.09$, $df = 16$, $P \ll 0.01$). Others have reported similar results. Smith (1973, 1985) found that the ratio of the abundance of Pacific sardine larvae to sardine eggs in ichthyoplankton net tows was less than the corresponding ratio in northern anchovy, indicating that the mortality rates of larval sardines are indeed higher than those of larval anchovy. Smith et al. (1989) found higher mortality in sardine eggs than in Peruvian anchovy eggs in the same water mass.

Analysis of swimming energetics (Webb and Weihs 1986) and distribution of prey items (Vlymen 1977) also suggest greater mortality rates for faster growing larvae. Faster growing larvae must search greater volumes of water to obtain more food, and in so doing are at greater risk to predation than slower growers. On the other hand, lesser mortality rates for faster growing fish larvae are suggested by the relationship of particle size and mortality (Brooks 1968; Peterson and Wroblewski 1984; Kirkpatrick 1984), i.e. mortality in the sea is inversely related to body size. Faster growing fish larvae are subject to high mortality rates associated with small size but for a shorter

period of time than slow-growing larvae. Because the mortality of the faster growing sardine larvae is greater than the mortality of the slower growing anchovy larvae, the energetic arguments of Webb and Weihs (1986) and Vlymen (1977) are supported by this analysis.

Behavioral differences observed in the laboratory may explain the observed differences in mortality rates. At a given age, fewer sardine larvae than anchovy larvae escape attack by adult anchovy (Butler and Pickett 1987). If predation contributes a significant fraction of larval mortality, then the greater vulnerability to visual predators of sardine larvae would contribute to a greater mortality rate. The observation by Brownell (1985) that Cape anchovy, *Engraulis capensis*, cannibalize larvae and juveniles as large as 50% of their own length supports the idea that anchovy may contribute to sardine mortality at lengths longer than the 20 mm considered here.

Stable Ocean Hypothesis

The lack of correlation between the number of calm days at 27°N, 116°W and larval sardine mortality rates does not support the hypothesis that periods of calm weather are necessary for the survival of all larval fish. This lack of correlation may be due in part to the absence of a strong signal in wind speed at this location. In the California Current regions, most of the strong wind events are related to storms which originate in the North Pacific. These storms reach southern California only infrequently, and their effects are less in northern Baja California.

In order for mixing to have an impact on larval mortality rates or recruitment, it must affect a significant portion of the population. Because most sardine spawning was well to the south of Point Conception, it is unlikely that storms and the resulting instability of the water column play a major role affecting the survival of sardine larvae in the California Current. Thus, Peterman and Bradford's (1987) conclusion that Lasker's stable ocean hypothesis accounts for a significant fraction of the interannual variability in the mortality of anchovy larvae is not extended to sardine larvae by this analysis.

The stable ocean hypothesis may explain the mortality of first-feeding anchovy larvae, but it does not explain recruitment

(Peterman et al. 1988). Evidence that starvation is not an important factor after the first-feeding stage has been presented by Owen et al. (1990) who found no difference in starvation rates, growth rates, or mortality rates of anchovy larvae in two areas of the California Current characterized by contrasting biomasses of plankton as collected by 45- μ m-mesh nets. Lack of variation of larval anchovy growth rates between El Niño and non-El Niño years also casts doubt on the starvation hypothesis (Butler 1989).

Transport Hypothesis

Hjort's (1913) hypothesis that year class strength was determined early in life of fishes and that the sources of mortality of larval fish were due to starvation of first-feeding larvae or to transport out of feeding grounds has been the basis of much fisheries research. Based on the analysis of larval mortality rates and transport both southerly and offshore, there is no support for either component as a mechanism determining sardine larval mortality rates. Nor is there support for the hypothesis that offshore transport affects recruitment success to the adult population.

Whether southerly transport affects recruitment is debatable. The sea level anomaly, as an index of transport, has been correlated with recruitment to the Pacific mackerel population (Sinclair et al. 1985). Recruitment of 2-yr-old sardines is also correlated with the sea level anomaly (MacCall 1979 and above). This correlation may be due to the increased availability of 2-yr-old sardines off Southern California during the El Niño years of 1957-58 (MacCall 1979). If the El Niño years are excluded from the analysis, there is no correlation. However, eliminating El Niño years might exclude the conditions which would produce the hypothesized effect.

Examination of the aged landings (MacCall 1979, table 1) suggests that either the 1957 and 1958 year-classes were over-represented or those year-classes incurred greater than normal mortality in the ensuing years. Furthermore, if the sea level anomaly is compared with recruitment, using a 2-yr time lag to test the effect of southerly transport during the year that the eggs were spawned, then the correlation is negative, but not significant. Thus, Hjort's (1913) second hypothesis that transport away from nursery grounds is not strongly supported by this analysis.

Predation Hypothesis

Although the predation hypothesis is supported by the evidence presented here, none of the other hypotheses can be categorically rejected. However, no correlation other than with predators could explain the observed trend in larval mortality rates. Predation is also consistent with the observed trend in recruitment.

Cannibalism of eggs and larvae in anchovies is well known (de Ciechomski 1967; Hayasi 1967; Loukashkin 1970; Hunter and Kimbrell 1980; MacCall 1980; Santander et al. 1983; Alheit 1987; Smith et al. 1989). In the northern anchovy, cannibalism can account for 20-28% of the observed egg mortality (Hunter and Kimbrell 1980). In an analysis of cannibalism by the Peruvian anchoveta, Alheit (1987) found that cannibalism accounted for 22% of the egg mortality. Stomachs of Pacific sardine in the same area also contained anchoveta eggs. On a per-weight basis, Alheit (1987) estimated that sardines may consume as many as or more anchoveta eggs than the ancho-

veta. Together, the two species may account for about 50% of the daily anchoveta egg mortality.

If northern anchovy filter their own eggs, then they must certainly also feed on other fish eggs and larvae. Perhaps because of the thin integument of larval fish and because of rapid digestion rates, fish larvae are rarely found in the stomachs of anchovy (Hunter and Kimbrell 1980). Fish eggs reported in the stomachs of anchovy by Loukashkin (1970) were not identified. Northern anchovy occurs with sardine during spawning (Ahlstrom 1967) and thus could consume significant numbers of eggs and larvae. Cannibalism is also consistent with the observed trend in anchovy larval mortality rates, but this effect was discounted by Peterman and Bradford (1987) due to the confounding of the slope (mortality) and the intercept (spawning biomass) of larval production and because mortality was more strongly correlated with water column stability. However, Pepin (1987) extended the analysis to predator to prey ratios and found that anchovy larval mortality rates were related to predation by total pelagic fish biomass.

Smith (1985) listed three situations in which cannibalism by schooling pelagic fishes would be effective in population control: (1) directed filtering behavior on dense aggregations of eggs, (2) encounter with other schools' patches of eggs, and (3) anchovy population switching from biting to filtering behavior. The correlation of mortality rates with predator to prey ratios is support for the later scenario. The same three situations also apply to predation of schooling pelagic fish on the eggs and larvae of other fishes, and the latter two scenarios are consistent with the observed trends in Pacific sardine larval mortality and northern anchovy biomass.

Conclusions

Competition between adults (Murphy 1966) or between larvae (Marr 1960) has been suggested as the important interactions between sardine and anchovy. Between 1951 and 1967, it is unlikely that the abundance of either species or their total biomass could have affected their food supply significantly. The biomass of sardines is far below its maximum in the 1930's. It is also unlikely that the biomass of fish larvae ever affects larval food densities (Cushing 1983). But Jones (1989) argued that larval fish may consume a significant fraction of secondary production and that resource limitation is possible for larval fish. Owen et al. (1990) found no difference in larval growth rates between sites with contrasting microzooplankton densities. The correlation of larval sardine mortality with anchovy abundance indicates an important interaction between the two species which has not been documented previously.

The decline of the Pacific sardine fishery during the late 1940's and 1950's has been ascribed to overfishing during periods of poor recruitment (Clark, in Clark and Marr 1955; Murphy 1966; MacCall 1979). Marr (1960) found no obvious relationship between parent stock size and recruitment and concluded that environmental change was responsible for recruitment failure and the decline of the Pacific sardine stock. Iles (1973) also suggested climatic change as the agency of recruitment failure of the Pacific sardine.

Analyzing the waning years of the sardine fishery, MacCall (1979) noted a "string of poor recruitments since 1958. . . remarkable in its duration and magnitude." The increase in larval mortality rates during the time period is also remarkable for its duration and magnitude. The correlation of the larval mortality rates with anchovy biomass indirectly sug-

gests that the two species interact by predation. Anchovy predation on eggs and young larvae (<20 d) would produce the observed correlation between anchovy biomass and larval sardine mortality rates. Predation on older larvae (>20 d) and young juveniles would explain the negative correlation between sardine recruitment and the combined biomass of pelagic fishes and would largely explain the string of poor recruitments observed in the 1960's.

Of the three hypotheses advanced to predict larval mortality rates, water column stability and starvation of larvae, transport away from nursery grounds, and predation, only predation explains the observed trends in larval sardine mortality rates and recruitment success.

Acknowledgments

Andrew Bakun, Pacific Fisheries Environmental Group, provided wind speed data. Rich Methot provided estimates of the northern anchovy biomass. I especially thank Nancy Lo for her assistance and both Paul Smith and John Hunter for their advice. Waldo Wakefield, Gail Theilacker, Al Myrick, and William Bayliff (Inter-American Tropical Tuna Commission) read and commented on the manuscript.

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